PROC. BIOL. SOC. WASH.
102(2), 1989, pp. 385–393

AEGLA DENTICULATA LACUSTRIS, NEW SUBSPECIES, FROM LAKE RUPANCO, CHILE (CRUSTACEA: DECAPODA: ANOMURA: AEGLIDAE)

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Abstract.—A subspecies of *Aegla denticulata* Nicolet, 1849, is described as *A. d. lacustris.* The new subspecies is restricted to the preandean Lake Rupanco, in the River Bueno basin, Osorno Province, Chile, while the nominate subspecies is widespread in small, moderately fast running streams in the Central Valley of Valdivia, Osorno, and Llanquihue provinces. *A. d. lacustris* differs from *A. d. denticulata* in having markedly more prominent spinulation along the branchial margins of the carapace and upon the chelipeds.

Aegla denticulata Nicolet, 1849, is one of the best known Chilean aeglids. Its morphotype is easily distinguished from that of all other species of *Aegla* Leach (Schmitt 1942). Extensive collections made by the author in central southern Chile have shown that *A. denticulata* ranges between Cautín and Chiloé (Jara 1980 and unpublished data), living in small to medium-sized rivers along the Chilean Central Valley.

A large population of *A. denticulata* was found occupying the sublittoral of Lake Rupanco (Osorno Province). When I compared the specimens collected in the lake with those collected in rivers, it became apparent that the lake specimens differed markedly in the expression of the carapace ornamentation. The spininess of the lacustrine specimens is remarkably more prominent than that of the riverine animals.

Since this highly ornamented morphotype was found to be restricted to Lake Rupanco, this variant population was considered to represent a geographic isolate of *A. denticulata,* thus deserving a description as a new subspecies (as defined by Mayr 1969).

Aegla denticulata lacustris, new subspecies

Fig. 1a, c, e, g, i, k, m, o

Holotype.—Instituto de Zoología, Universidad Austral de Chile (IZUA), IZUA C-686, adult male, Huillín Cove on northwestern shore of Lake Rupanco (40°49′S; 72°28′W), Chile, 25 m depth, baited crab trap, 30 Apr 1984, coll. C. G. Jara.

Allotype.—Adult female, 8 Sep 1984, IZUA C-686, same locality, collecting device and depth as for holotype.

Paratypes.—IZUA C-687; eight adult males (P1 to P8), 30 Apr 1984; eight adult females (P10 to P16), 8 Sep 1984; one ovigerous female (P9), 3 Apr 1984; same locality, collecting device and depth as for holotype. Four juveniles (P17 to P20), 7 Sep 1984, 18 m depth, Scuba hand collection.

Diagnosis.—External margin of anterolateral lobe of carapace with row of tiny spinules; summit of middorsal carina with irregular narrow band of minute scales; distodorsal margin of merus of chelipeds with transverse row of small but well defined spines; posterior branchial margin of carapace definitely denticulate; summit of dorsolateral carina on second abdominal epimeron with irregular row of scales; laterodorsal area of tergum of second abdominal segment markedly protuberant, its apex scaly; dorsum of merus and carpus of second to fourth pereiopods clearly denticulate; denticles on anterior branchial margin conical; palmar crest of chelipeds deeply incised.

Description.—Carapace ovoid, markedly

elevated along middorsal line forming well defined keel extending from rostrum to posterior margin of carapace. Dorsal surface of carapace and abdomen finely punctate; when dry, polished and glossy brilliant. Short stiff setae protrude from punctae, some together with minute lenslike scales.

Rostrum prominent, straight, broad-based, extended in horizontal plane but sometimes slightly recurved at tip. Form varying, from strictly triangular to ligulate. Rostral margins well defined and slightly upturned, fringed with row of closely packed minute conical scales pointing towards rostral apex. Distal third flattened, merging with rostral carina into acute conical apex. Rostral carina narrow, sharp, with row of minute scales not reaching rostral apex. Proximal end of rostral carina marked by two small pits just in front of protogastric lobes. Epigastric prominences blunt, slightly protuberant. Protogastric lobes pronounced, their uppermost part with small field of lenslike scales. Orbits wide, deep, limited at external angle by acute conical orbital spine; short row of acute scales just posterior to orbital spine on orbital margin. Anterolateral angle of carapace produced as strong acute conical spine extending from broad flattened anterolateral lobe. Tip of spine reaching at least middle of cornea. Extraorbital sinus a deep V-shaped notch. External margin of anterolateral lobe with row of small acute spines variable in number and size. Free angle of first hepatic lobe produced as strong, acute, dorsally recurved spine bearing from two to five scales at base. Second and third hepatic lobes also well marked and bearing spiniform scale at frontal angle and row of minute scales along free margin. Gastric area quite elevated at midline, then sloping down both sides of carapace, reaching broad concavity at dorsum of hepatic lobes. Uppermost part of middorsal carina rugose and scaly throughout. Cervical groove distinctly marked but not deeply incised.

Anterior branchial area raised towards midline but leveling into horizontal plane towards free margin. Frontal angle produced as one or two coalescent, strong, sharply acute conical spines. Anterior branchial margin laterally expanded in row of from seven to nine single or multiple tipped prominent sharply acute denticles that scarcely decrease in size from anterior to posterior. Row of 9–11 tiny conical scales mounted atop small tubercles along external branchial suture.

Posterior branchial area with complicated topography; inner part raised and leveled with cardiac area, then sloping towards lateral margin, which rises again above marginal zone leaving behind wide longitudinal trough. Margin markedly expanded in row of 9–11 clear-cut conical, single or multiple tipped, markedly recurved spinelike denticles. Anteriormost and posteriormost denticles smallest. At limit between anterior and posterior branchial margin, first posterior denticle overlaps last anterior denticle. Posterior margin of carapace thick, more protuberant at middle section, which occasionally forms broad based tubercle.

Abdominal terga deeply sculptured. Median section markedly protuberant especially at frontal edge, which forms moderately sharp transverse carina. On pleural area, near laterodorsal pit on second abdominal segment, dorsal surface raised frontally forming rotund broad-based prominence bearing at summit from two to five tiny scales. Anterolateral angle of second abdominal epimeron produced as strong spine tipped with sharp conical scale. It stands at frontal end of narrow oblique carina extending over anterior two thirds of epimeral dorsum. Crest of carina with row of closely juxtaposed minute scales decreasing in size posteriorly. Lateroventral angle of epimeron acute; if rounded off, bearing two or three acute scales. Lateral angle of third and fourth epimera sharply acute. Telson plate dimerous, subpentagonal.

Third thoracic sternum broad, its ventral surface protuberant, rugose, bearing tiny

scales at frontal tip and sometimes one or two scales along median line. Fourth sternum with long robust spinelike tubercle markedly compressed into sagittal plane, tipped with one major and two to three minor scales. Fifth sternum slightly swollen but not forming tubercle. Frontal margin of sixth sternum bearing one or more tiny scales in transverse row.

Chelae subtriangular to ovoid, dorsoventrally depressed. Dorsal surface quite punctate and covered by numerous small scales atop minute tubercles. Scales on proximal external surface lenticular and flat, then becoming more acute and prominent towards finger tips. Two low, relatively narrow ridges on dorsal surface of chelae, one starting from upper articulating condylus at carpus-propodus joint and ending at condylus of propodus-dactylus joint. Uppermost part of this ridge with irregular row of scales larger on proximal end. Second ridge along median line of chela extending from carpus-propodus joint to proximal end of cutting edge of fixed finger; it is marked by straight row of acute scales. Finger cutting edges closely fitted along distal two thirds but with small gap at proximal third. Dorsal edge of dactylus with sharply prominent conical tubercle at proximal end, followed distally by row of smaller acute tubercles or enlarged scales. Palmar crest semicircular in outline, deeply incised, formed by from two to three stout single or multiple tipped acute spines arising from thick bases. Smaller spines or spinules attached to basis of body of main spines. Frontal margin of propodus above propodus-dactylus joint with acuminate tubercle; spinules are found on both sides of it. Ventral surface of chela with low but well defined carina between lower condylus of carpus-propodus joint and tip of fixed finger.

Carpus strongly armed. Carpal crest with two or three sharp, long, robust spines; one or two small tubercles behind proximal spine. Carpal lobe spiniform, as long as second spine of carpal crest. Row of from five to seven spiniform tubercles external to and parallel to carpal crest. Second row of smaller but acute tubercles external to above row. Distodorsal margin of carpus fringed by acute scales. Ventral surface with acute conical spine as long as second spine in carpal crest. Distoventral angle below carpus-propodus condylus with small spiniform tubercle.

Dorsal margin of merus with from five to eight single or multiple tipped distinct spines decreasing in size proximally. Spinules occasionally present among bases of spines. External face roughened by scales, mostly on upper half. Distodorsal vertex with large, somewhat flattened procurved spine longer than the longest in row behind. Margin external to it with row of sharp conical spinules. Inner ventral margin with from two to five spiniform tubercles in row behind single or double tipped spine at distal end. External ventral margin scabrous or tuberculate. Distal end with spine as large as that on inner ventral margin. One to three small acute tubercles variable in size in front of latter. Articular lobe at distalmost end of same margin spiniform. Inner ventral margin of ischium with low broad nodule on proximal end. Distal end with conical spine. Between both ends from one to four acuminate tubercles variable in size. Distodorsal angle with short but acute spine slightly displaced over outer surface.

Distoventral margin of ischium of pereiopods fringed with minute scales; one of these scales occasionally larger just behind ischiomeral joint. Dorsal margin of merus with row of small but clear-cut acute denticles decreasing in size proximally; distodorsal angle noticeably spiniform; ventral margin scabrous bearing minute scales intermingled with short stiff setae. Dorsal margin of carpus also with small denticles; distodorsal angle spiniform. Dorsal and ventral margin of propodus with dense narrow band of scales and setae. Dorsal surface of all pereiopodal articles except dactyl micronodulose and squamous.

Color (in life).—Dorsum of cephalotho-

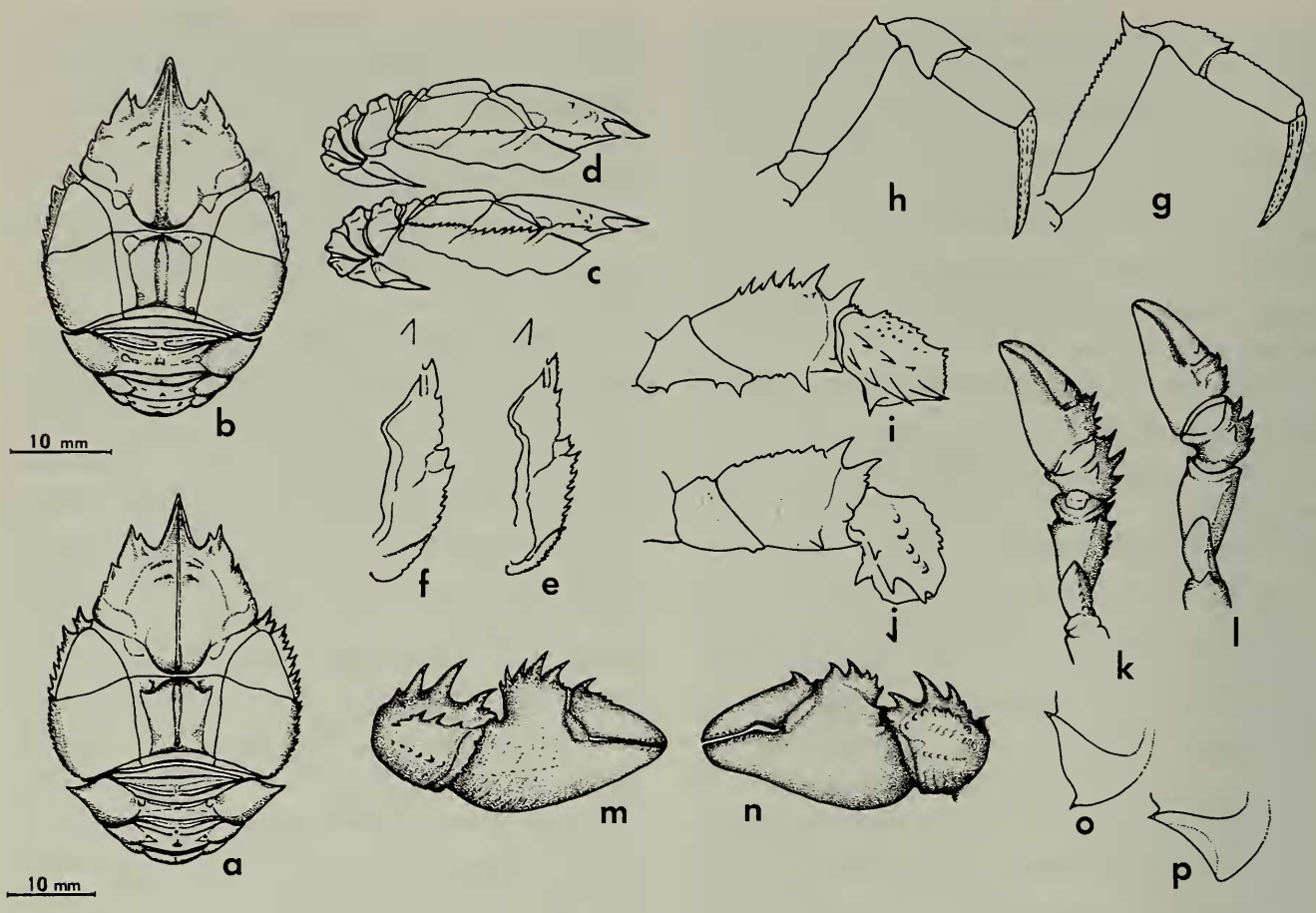

Fig. 1. *Aegla denticulata lacustris* (holotype), a, c, e, g, i, k, m, o; *A. denticulata denticulata* Nicolet, 1849, male 25.7 mm CL from River Puquitre (IZUA C-686), b, d, f, h, j, l, n, p. a, b, Dorsal view of carapace; c, d, Lateral view of carapace; e, f, Left margin of carapace (ventral); g, h, Second right pereiopod; i, j, Inner view of ischium and merus of left cheliped, carpus seen from above; k, l, Ventral view of right cheliped; m, n, Chela and carpus (dorsal); o, p, Lateral view of left second abdominal epimeron.

rax and abdomen highly variable among individuals, ranging from orange-yellow to almost black. Though variation between both extremes is continuous, an attempt was made to quantify the frequency with which different patterns appear in the population. The following patterns were defined and their frequency recorded (Table 1):

Pattern A: Dorsum of cephalothorax and abdomen uniformly orange-yellow to terracotta, occasionally scattered with small, irregular, dark brownish spots.

Pattern B: Dorsum of cephalothorax and abdomen variegate; extensive reticulate dark green or dark brown design on a khaki or light brown background.

Pattern C: Dorsum of cephalothorax and abdomen uniformly dark greenish brown or dark reddish brown.

Pattern D: Dorsum of cephalothorax and abdomen variegate; small to extensive dark green patches on a lighter blue-green or brown-green background.

Pattern E: Dorsum of cephalothorax and abdomen variegate; small but numerous yellowish or light greenish brown spots on a uniform dark brown background; in some specimens dorsal carina bluish tinged.

Pattern F: Dorsum of cephalothorax and abdomen variegate; ample irregular blue-black or brown-green-black patches on a lighter blue-gray or gray-violet background.

In all specimens, the dorsal surface of the pereiopods has the same color pattern as the dorsum of the carapace but with darker stripes across the carpus and merus. The distal half of the chelae is always white or yellowish-white, contrasting markedly with

the darker proximal half. The ventral surface of the body and appendages is milky white or slightly yellowish. The articular membrane of the appendages is bright purple-red.

In formalin fixed specimens, the dorsum of the carapace is wine-red in color, whereas in alcohol preserved specimens the color changes to light brown or tan.

Variation and measurements.—Making allowances for minor variation in the size and number of spines along the upper margin of the merus and dorsum of the carpus of the chelipeds, adults in the type-series are quite similar. Juveniles (P17–20) have many features of the adult morphotype only slightly developed (spines, tubercles, etc.) but are still recognizable. The major difference between adults and juveniles is that in the latter the tegumental scales are replaced by short fine setae, most notably on the dorsum of the chelae and on the abdominal terga.

Somatometric data of specimens in the type-series are give in Table 2. Measurements were made with calipers to the nearest 0.1 mm; symbols for the morphometric characters in the first column are given by Jara & López (1981).

Distribution.—Known only from the type locality. Attempts to collect *A. denticulata lacustris* in Lake Puyehue, 12 km to the north of Lake Rupanco, failed. In July 1984, during the winter high-water period of Lake Rupanco, two small specimens (LC about 10 mm) were collected in a protected site at the bank of River Rahue, 150 m from the outlet of the lake. These specimens were most probably washed out from the lake by the effluent current.

Habitat and natural history.—Lake Rupanco is the southernmost of three major preandean piedmont lakes included in the River Bueno basin, and is the fifth in size among Chilean lakes. It has a maximum depth of 274 m and an area of 233.4 km^2. Limnologically, it is an oligotrophic, cold temperate monomictic lake that circulates at 9.6°C in midwinter and reaches 19°C at epilimnion in summer. Dissolved oxygen is high throughout the year (9.1 to 12.2 mg/liter); conductivity is low (40.6 to 54.0 μS) and calcium is scarce (2.1 to 4.8 mg/liter) (Campos et al. 1985). Lake Rupanco lies at 118 m above sea level. Its eastern half is surrounded by massive mountains and volcanoes (Puntiagudo and Casablanca) of the Andes Cordillera. Its affluents are small to medium-size rivers of pluvial or pluvio-glacial regime. Its effluent (River Rahue) discharges about 100 m^3/sec on the average (Campos et al. 1985). Lake Rupanco is of glacial origin. The inferred chronology of the regional glacial events suggests that Lake Rupanco attained its present form about 11,000 years B.P. (Mercer 1972).

Table 1.—Frequency of color patterns in *A. denticulata lacustris*, from Lake Rupanco. Color patterns defined in text. Sample size: 116 adult specimens collected at 25 m depth on 30 Apr 1984, with baited traps. Sex unrecorded.

Pattern	Frequency	
	Absolute	Relative (%)
A	5	4.31
B	11	9.48
C	3	2.59
D	39	33.62
E	29	25.00
F	29	25.00

Underwater observations, made by the author between 0 and 30 m depth at Huillín Cove, showed that *A. d. lacustris* occupies the sublittoral zone from 8 m depth downward. Its vertical distribution appears closely related to that of the soft substrate on which crabs alternatively walk and collect particles with their maxillipeds. Activity is markedly higher at night, while during the day a great proportion of the crabs rest buried in the substrate. No data are available on the diet of *A. d. lacustris*, but it can be presumed that they feed on fine-grained detrital matter, though they were seen consuming a dead fish lying on the bottom of the lake. Berried females appear at the end of the summer period (March), and the release of newborn crabs from the brooding abdominal cham-

Table 2.—Somatometry of *A. denticulata lacustris,* new subspecies, type-series. All measurements in mm. M = male; F = female; F* = ovigerous female; Holo = holotype; Allo = allotype; P1 to P20 = paratypes. CL, carapace length, distance between rostral apex and posterior margin of cephalothorax; RL, rostral length, distance between rostral tip and midpoint of transversal line tangent to deepest point of orbital margins; PCL, precervical length, distance between rostral tip and midpoint of cervical groove; FW, frontal width, distance between tips of anterolateral angles of carapace; PCW, maximum precervical width, distance across third hepatic lobes; CW, maximum carapace width; LCL, left cheliped length; RCL, right cheliped length; L2PL, length of second left pereiopod; L2DL, dactylar length of second left pereiopod; L4DL, dactylar length of fourth left pereiopod; TL, telson length.

Specimen:	Holo	Allo	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20
Sex:	M	F	M	M	M	M	M	M	M	M	F*	F	F	F	F	F	F	F	M	F	F	F
CL:	31.5	28.8	37.1	31.2	29.6	29.3	29.2	28.8	29.3	27.8	28.2	29.7	26.8	29.0	26.1	25.9	26.9	25.2	11.6	10.7	9.2	8.2
RL:	7.1	7.0	8.7	7.0	6.4	6.5	7.1	7.0	7.0	6.4	6.9	7.0	5.8	7.0	5.8	6.1	6.2	5.8	2.6	2.6	2.1	2.0
PCL:	22.0	19.9	25.2	21.8	20.3	20.2	20.8	20.0	20.3	19.3	19.4	20.8	18.1	20.0	18.4	17.9	18.0	17.3	8.0	7.5	6.5	5.9
FW:	10.0	9.0	11.3	10.2	10.0	10.0	9.5	9.1	9.1	9.0	8.9	9.0	9.2	9.2	8.9	8.1	8.2	8.3	4.0	3.9	3.3	3.0
PCW:	18.9	16.7	22.3	19.0	18.0	18.0	17.0	18.0	17.7	17.0	16.5	18.1	16.9	17.7	16.3	15.8	16.1	15.2	7.5	6.7	6.0	5.1
CW:	30.2	26.7	35.4	29.7	29.0	28.4	26.9	28.5	27.3	25.9	26.7	29.4	26.5	27.3	25.6	25.5	25.5	24.6	10.1	9.0	7.9	7.0
LCL:	40.2	32.0	48.4	38.2	38.5	33.8	36.3	35.5	34.0	34.8	32.0	34.1	31.8	33.0	30.0	29.7	29.0	30.0	13.3	11.8	10.2	9.2
RCL:	39.0	31.3	42.9	38.0	37.1	33.0	35.1	34.4	33.5	33.0	31.0	34.0	31.3	32.0	29.7	28.9	28.6	29.1	13.3	11.8	10.3	9.2
L2PL:	43.1	—	48.6	42.3	41.2	—	40.2	39.3	39.1	38.0	37.0	40.0	37.0	38.1	35.9	34.6	33.4	34.2	15.9	13.8	11.5	11.1
L2DL:	9.9	—	12.0	9.8	9.6	—	10.3	9.3	9.6	9.0	8.7	10.2	8.7	9.0	8.2	8.4	7.8	8.0	4.0	3.4	3.1	2.7
L4DL:	—	9.8	11.8	10.2	10.0	—	10.0	—	9.9	9.3	8.8	10.2	8.4	8.9	8.2	8.4	—	8.2	4.0	3.5	3.1	2.9
TL:	6.0	6.0	7.0	6.2	6.0	5.8	6.0	5.8	5.8	5.4	6.8	6.8	6.7	6.1	6.2	5.4	5.2	5.3	2.4	2.2	2.0	2.0

ber of the females occurs at the beginning of the subsequent spring (October).

At Lake Rupanco, *A. d. lacustris* coexists with *Aegla abtao* Schmitt and the crayfish *Samastacus spinifrons* (Philippi). *A. abtao* occupies the littoral zone and the upper sublittoral to 15 or 20 m depth. However, below 4 m only large adult males are found. The bulk of *A. abtao*'s population lives among and under big stones and boulders in the littoral. *S. spinifrons* is found in the sublittoral at least down to 80 m depth, only on soft substrate. Biological interactions among these three species of decapod crustaceans are suspected but the only one observed so far is predation by large *A. abtao* males upon juveniles of *A. d. lacustris*. Other faunal components of the benthic community at Lake Rupanco are freshwater mussels of the genus *Diplodon* and *Pisidium*, aquatic snails of the genus *Chilina*, the minute janirid isopod *Heterias exul* (Bowman et al. 1987), amphipods, acari, oligochaetes, chironomid larvae and caenid ephemeropteran nymphs.

Etymology.—The trivial name *lacustris*, from Latin, alludes to the fact that this subspecies of *A. denticulata* is apparently restricted to a lentic environment.

Comparison.—To compare lacustrine and riverine specimens of *A. denticulata*, four crabs (two males and two females) from the series from which the neotype of *A. denticulata* was drawn, National Museum of Natural History (USNM 169096 = USNM 80021) (Schmitt 1942) were examined. Additionally, 30 males (LC 18 to 26 mm) collected in rivers Puquitre and Remehue, 8 km north of Osorno city, and 50 males (LC 23 to 33 mm) from Rupanco were examined and measured. One male from the Puquitre (IZUA C-686) was employed for preparing Fig. 1b, d, f, h, j, l and p.

A. denticulata lacustris is very similar to the nominate subspecies *A. denticulata denticulata* Nicolet, 1849, from which it departs by the morphological features already mentioned in the Diagnosis. Additionally,

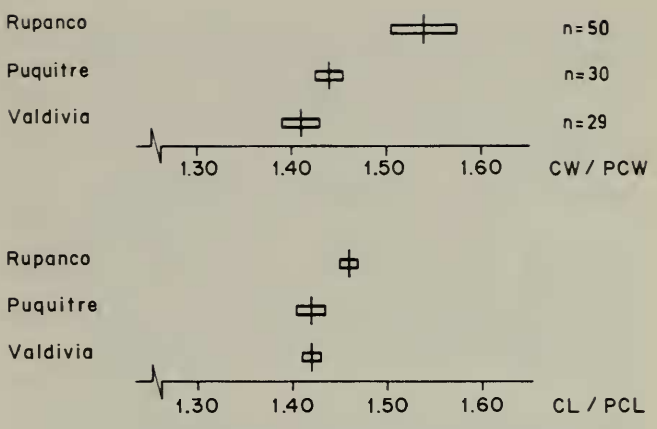

Fig. 2. Somatometric comparison of males of *A. denticulata lacustris* (Rupanco) and males of *A. denticulata denticulata* (Puquitre and Valdivia). Sample labeled Valdivia is a composite made of individuals collected all over the Valdivia River Basin (Jara 1980). Vertical line: mean value of somatometric proportion; open rectangle: confidence interval for the mean (P = 0.05). Above: proportion between maximum carapace width (CW) and maximum precervical width (PCW). Below: proportion between carapace length (CL) and precervical length (PCL).

A. d. lacustris differs from *A. d. denticulata* in the following respects: ridge of dorsal carina sharper; dorsal profile of carapace less inflated (cf. Fig. 1c, d); external margin of anterolateral lobe of carapace minutely denticulate; denticles along ridge of merus of chelipeds longer and sharper; tubercles of middorsal row of carpus definitely spiniform; spine of carpal lobe longer and more slender (cf. Fig. 1i, j); carpal ventral surface less hairy; denticles of palmar crest longer and slender; ventral angle of second abdominal epimeron often produced into short acute spine (cf. Fig. 1o, p).

Because of the slender and clear-cut appearance of the main spines of its carapace, together with the cleanness of the carapace surface, *A. d. lacustris* is reminiscent of another lacustrine species, *A. rostrata* Jara, but differs from it in that *A. rostrata* lacks the dorsal carina and the median tubercle on the fourth thoracic sternum. On the other hand, *A. d. lacustris* lacks the distinctive stylet-like rostrum of *A. rostrata*.

In Fig. 2 the average and confidence in-

tervals ($P = 0.05$) of two somatometric proportions for riverine (Puquitre and Valdivia) and lacustrine (Rupanco) samples are compared.

Remarks.—Though at first sight the Lake Rupanco morphotype is clearly differentiable from the riverine morphotype found elsewhere in southern Chile, key characters that differentiate the two forms appear elusive. With the exception of the row of tiny spinules along the external margin of the anterolateral lobe of the carapace, the band of tiny scales on the ridge of the dorsal carina, and some other minor details, every morphological attribute in *A. d. lacustris* has its counterpart in *A. d. denticulata.* The difference is a matter of degree of expression rather than of difference of attributes. The Rupanco's morphotype appears to be an elaborate manifestation of the attributes found in riverine specimens. The decision to assign the Lake Rupanco population a subspecific status is supported by the fact that Lake Rupanco's population is, on geographical and ecological grounds, an outlier as compared to the remaining populations of the species. In fact, Lake Rupanco is the easternmost locality where *A. denticulata* has been reported in the River Bueno basin, and the only one in which the species inhabits a lentic environment. The possibility that Lake Rupanco's population has already attained reproductive isolation with respect to the riverine populations, and therefore qualifies as a different species, remains an open question.

As mentioned elsewhere (Jara 1986), the trend towards profuse spinulation in *Aegla* seems to be correlated with living in lentic environments. The prominent ornamentation seen in *A. d. lacustris* lends support to this hypothesis. However, no explanation is available for this overgrown spinulation, neither from the ecological nor from the genetical point of view. Profuse spinulation in *A. d. lacustris* may well be an adaptive response to its immediate biotic or abiotic environment. Otherwise, spinulation could be a by-product of genetic changes related to presently unknown factors. Comparison of *A. d. lacustris* and *A. d. denticulata* life histories could be illuminating in these respects.

If the geographical and chronological relationship between rivers and lakes in southern Chile is considered (see comments in Jara 1977, 1982, 1986), it appears evident that lacustrine populations of aeglids descended from riverine stocks. These last would have withstood the Quaternary glacial events in non-glaciated areas, located along the western border of the Chilean Central Valley and in the Coastal Cordillera (Illies 1960). That scenario implies that aeglids could have colonized the lakes rather recently (in geological time). Mercer (1972) estimates that lakes Llanquihue and Rupanco became free of ice about 11,000 years B.P. Therefore, to colonize the Andean lakes, aeglids had to advance from west to east, along the rivers that drained the newly formed lakes. Most probably, the forerunners of *A. d. lacustris* were specimens of *A. d. denticulata,* which could have entered the young Lake Rupanco from rivers of the Central Valley of Osorno Province. If spinulation of *A. d. lacustris* is a derived condition related to modifications of the former riverine invader's genome, one could expect to find evidence of these changes by comparing population samples of both subspecies by suitable techniques (protein electrophoresis, caryological analysis, etc.) (Wiley 1981).

Acknowledgments

The author thanks René Navarro and Gonzalo Aguilar for their assistance during the field work at Lake Rupanco; Dr. Raymond E. Manning of the National Museum of Natural History for the loan of four specimens of *A. denticulata*; Mrs. Patricia Araya and an anonymous reviewer for correcting the MS; Dr. Thomas E. Bowman for making available to the author his paper on *Heterias*

exul; and Dirección de Investigación y Desarrollo, Universidad Austral de Chile, for funding field work through grant RS-83-39.

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